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Published in:
Evolution

DOI:
10.1111/j.1558-5646.2010.01046.x

Publication date:
2010

doi:10.1111/j.1558-5646.2010.01046.x

FREQUENCY-DEPENDENT SOCIAL DOMINANCE IN A COLOR POLYMORPHIC CICHLID FISH

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Received March 22, 2010
Accepted May 4, 2010

A mechanism commonly suggested to explain the persistence of color polymorphisms in animals is negative frequency-dependent selection. It could result from a social dominance advantage to rare morphs. We tested for this in males of red and blue color morphs of the Lake Victoria cichlid, *Pundamilia*. Earlier work has shown that males preferentially attack the males of their own morph, while red males are more likely to win dyadic contests with blue males. In order to study the potential contribution of both factors to the morph co-existence, we manipulated the proportion of red and blue males in experimental assemblages and studied its effect on social dominance. We then tried to disentangle the effects of the own-morph attack bias and social dominance of red using simulations. In the experiment, we found that red males were indeed socially dominant to the blue ones, but only when rare. However, blue males were not socially dominant when rare. The simulation results suggest that an own-morph attack bias reduces the social dominance of red males when they are more abundant. Thus, there is no evidence of symmetric negative frequency-dependent selection acting on social dominance, suggesting that additional fitness costs to the red morph must explain their co-existence.

KEYWORDS: **Cichlid fish, color polymorphism, frequency-dependent selection, Lake Victoria, male–male competition, sexual selection.**

Understanding the forces that maintain genetic and phenotypic variation within populations is a major challenge in evolutionary ecology, because both selection and drift tend to remove variation from populations (Ricklefs and Schluter 1993; Coyne and Orr 2004). Negative frequency-dependent selection (where rare types are favored by selection) can serve as a general mechanism maintaining variation (Fisher 1930; Heino et al. 1998; Sinervo and Calsbeek 2006). Many animal species display discrete variation in

color, such as fish (Seehausen 2000; Hughes et al. 2005), lizards (Calsbeek and Sinervo 2002a), frogs (Hoffman and Blouin 2000), and birds (Roulin 2004). Several types of advantages to rare types have been implicated in explaining the maintenance of such variability in color, such as a rare-morph survival advantage due to a decreased probability of predators detecting rare prey types (Olendorf et al. 2006; Fitzpatrick et al. 2009), a rare-male mating advantage due to a female preference for males bearing rare or novel color patterns (Hughes et al. 1999; Royle et al. 2008), or benefits of a rare-male mating strategy (Sinervo and Lively 1996; Bleay et al. 2007).

Male color is often used as a cue in aggressive interactions between males (Alatalo et al. 1994; Tynkkynen et al. 2004) and consequently male contest has been proposed to exert selection on male color (Seehausen and Schluter 2004; for recent review, see Grether et al. 2009). Selection arising from male contest competition or social hierarchy can be strong, because social dominance is often associated with priority of access to mates and resources and as a consequence dominant individuals are generally assumed to attain the highest fitness (West-Eberhard 1979; Berglund et al. 1996; Wong and Candolin 2005). When males preferentially direct aggression toward phenotypically similar rival males, rare male phenotypes would receive less aggression than common male phenotypes. This could generate frequency-dependent selection in several ways, such as rare morphs being more likely to gain higher dominance status as a result of reduced harassment from competing males (Mikami et al. 2004; Seehausen and Schluter 2004; Van Doorn et al. 2004). However, conspecific color phenotypes across a wide range of different taxonomic groups display asymmetric social dominance relationships in which one morph is more likely to defeat the other in dyadic interactions (e.g., Barlow 1983; Pryke and Griffith 2006; Healey et al. 2007), but it is unknown how this would affect the dynamics of rare-morph dominance advantages. The aim of this article is to examine experimentally the combined effect of own-morph aggression biases and different likelihoods of winning dyadic contests on frequency-dependent social dominance between competing color morphs in mixed group situations.

The haplochromine cichlid fish of the Great African Lakes are famous for their spectacular species diversity (for recent reviews, see Kocher 2004; Genner and Turner 2005; Seehausen 2006). Within genera, there is large variation in male color and this variation affects mate choice. Consequently, sexual selection by female mate choice has been implicated in their color diversification (Seehausen and Van Alphen 1998; Knight and Turner 2004). Sexual selection is expected to be particularly strong in haplochromines because their exclusively maternal brood care leads to an excess of males competing for unmated females (Kokko and Jennions 2008). In addition, male contest competition for access to females can exert selection on male color indirectly, because social status and territory size are important in mate choice (Maan et al. 2004; Dijkstra et al. 2008a), while color is used as a cue in intrasexual communication too (Dijkstra et al. 2005; Pauers et al. 2008).

The cichlid genus *Pundamilia* is widespread in Lake Victoria, containing many different sympatric color morphs and sibling species. Its Kissenda Island (Mwanza Gulf, Tanzania) population comprises two genetically determined incipient species or color morphs (red and blue; Seehausen 2009; Seehausen et al. 2008). Females show color-based mating preferences and mating is largely assortative with some gene-flow between red and blue as indicated by the occurrence of intermediate morphs (Haesler and Seehausen 2005). *Pundamilia* males defend territories mainly for mating purposes. Both morphs exhibit own-morph attack biases (Dijkstra et al. 2006, 2008b, 2009), but red males are more aggressive and tend to defeat blue in dyadic contests between the two morphs (Dijkstra et al. 2005, 2006, 2009). We varied the proportion of red and blue males in an assemblage situation and quantified agonistic behavior and social dominance of the two color morphs. We show that red males, but not blue males are dominant over the other morph when rare, in contrast to the predictions of the usual model of negative frequency-dependent selection where both rare types are favored. In addition, we confirmed the own-morph aggression bias in both red and blue males and the higher rate of aggression in red males than in blue males. We then constructed a simple model simulating the experimental situation in order to better interpret these findings. In this simulation, we explored how two different tendencies (own-morph aggression bias and different likelihoods of winning dyadic contests) and their interaction would affect the expected social dominance of the color morphs.

Material and Methods

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Fish and housing conditions

The Kissenda Island *Pundamilia* population consists of males expressing either blue or red nuptial coloration (Witte-Maas and Witte 1985; Seehausen et al. 1998). Laboratory crosses revealed that red and blue nuptial colors in *Pundamilia* are genetically determined, with hybrid crosses resulting in intermediate phenotypes (Haesler and Seehausen 2005; Van der Sluijs et al. 2008a). Red males at Kissenda Island tend to occupy a range of different water depths from shallow to deep, whereas blue males occur in the shallowest 3 m (Seehausen et al. 2008). Hence, their habitat is fully overlapping in shallow waters, making it likely that males of the two color morphs compete with one another over mating territories. More details on the study species can be found elsewhere (Seehausen and Van Alphen 1998; Stelkens et al. 2008; Van der Sluijs et al. 2008b).

All experiments used lab-bred offspring obtained from a stock of 41 wild-caught parental fish collected in June 2001 around Kissenda Island, Lake Victoria, Tanzania. Fish were reared in sib groups until approximately six months of age, when the first fish started to mature. They were then translocated into stock aquaria, containing males and females of both color morphs. The sides and the back of all aquaria were covered with black plastic. All aquaria were connected to a central biological filter system and water circulated continuously. The water temperature was kept at 25 ± 2°C and a 12:12 h light:dark cycle was maintained. All aquaria contained a substrate of gravel. Fish were fed with flake food at least once per day, and a mixture of ground shrimps and peas two times per week. Experimental males were sexually mature and at least 11 months of age. To reduce possible effects of prior experience, they were housed individually for at least one week before the experiment in aquaria measuring 90 × 36 × 30 cm ($l \times w \times h$), divided into eight compartments by polyvinyl chloride (PVC) screens. Since the screens were transparent, all males were able to see at least one other male of either color in an adjoining compartment, so avoiding social deprivation. Each compartment contained an opaque PVC tube that the fish used as a hiding place.

Experimental protocol

We used five experimental treatments, also referred to as "proportion of red males," which each had an assemblage of eight males in a single aquarium tank but in different ratios of red : blue as follows: (i) 1/8 proportion of red males (7 replicates): 1 red and 7 blue males; (ii) 2/8 proportion of red males (7 replicates); (iii) 4/8 proportion of red males (12 replicates); (iv) 6/8 proportion of red males (8 replicates); (v) 7/8 proportion of red males (8 replicates). The mean ± standard error (SE) weight of the fish was 15.94 ± 0.20 grams. To avoid effects of size asymmetry on dominance, fish in all five treatments were size-matched within groups (difference in weight between any male in an assemblage relative to the largest male, expressed as percentage of the lighter male [mean across assemblages ± SE] = 8.390 ± 0.095%; coefficient of variation mean ± SE = 0.054 ± 0.043, $n = 42$). The experimental aquaria, measuring 250 × 66 × 46 cm ($l \times w \times h$), contained three opaque PVC tubes in the middle of the left, central, and right part of the aquarium, standing upright on one end (diameter 15 cm, length 21 cm); these tubes mimic the type of rocky crevice that *Pundamilia* males in the wild use as the focal point for territorial defense (Dijkstra et al. 2008a).

We used 15 *Melanotaenia lacustris* (rainbow fish) as background fish in each experimental aquarium in order to disperse the aggression among experimental males, as in previous work (Dijkstra et al. 2009). We employed 49 red males (out of a total of 104) and 45 blue males (out of a total of 100) in more than one treatment, but no fish was used more than once within treatments (for a similar design, see Dijkstra et al. 2009). The interval between repeated use of the same male was a minimum of seven days. Prior to a test, we weighed all males to the nearest 0.01 g. We clipped males for individual recognition on their dorsal (two positions) and caudal fin (three positions), using scissors (Dijkstra et al. 2008a, 2009). These fin clips grow back in one week and cause no long-lasting damage to the fish.

We observed each assemblage on the first three days following release of the fish into the experimental aquarium. Each observation lasted 45 min, amounting to a total observation time of 135 min per assemblage. The males displayed the common aggressive behaviors of cichlids (Baerends and Baerends-Van Roon 1950). We recorded (using a tape recorder) aggressive interactions that resulted in a displacement, with the displaced fish being defined as the loser and the other as winner. Displacements could come about via (1) attack (i.e., one fish charging or chasing another fish) or (2) display (i.e., one or both fish showing lateral or frontal display, followed by fleeing of one of them).

We also noted every 15 min (three times per observation session) which males were displaying vertical bars on their flanks, which is a strong indicator of territoriality (Maan et al. 2004). Males that displayed these vertical bars during an observation session were defined as having territorial status.

Data analysis

In order to obtain an estimate of the relative dominance of red over blue, we calculated each individual's Win Ratio by counting the total number of wins relative to the total number of interactions for each day of observation separately (Smith and Metcalfe 1997). We opted for this measure of dominance, since total win-defeat experience of an individual is probably more important in terms of achieving territorial status and fitness than when this measure is corrected for the identity of the partner with which it fought. As a check on this approach, we also used an alternative method of estimating relative dominance that is more dyadic-relationship-based and is based on the Average Dominance Index (Hemelrijk et al. 2005). This change in analysis had little effect on the results (Fig. S1). Once we had calculated the Win Ratios, we took for each replicate assemblage the median Win Ratio, calculated for blue and red males separately (the median because the Win Ratios within assemblages were highly skewed) and used for red and blue males separately a hierarchical linear model (HLM) to test whether the Win Ratio was dependent on the proportion of red males, using the three daily scores nested within replicate assemblages and proportion of red males as covariate.

In analyzing the own-morph bias for aggression and the morph difference in rate of aggression, we only used data on attacks from the territorial males to reduce possible effects of differences in social status on the results. Territorial males receive fewer attacks than nonterritorial males, thereby potentially

compromising the estimates of attack biases when, for example, males of just one color morph were territorial. However, similar results were found using all males in the analysis (data not shown). The number of males per assemblage that were able to attain territorial status on at least one day of observation was on average 3.4 out of the eight.

To test whether the attacks by these territory holders were biased toward own-morph rival males, we calculated the proportion of attacks by territorial males toward their own morph, which is defined as the number of attacks against males of their own morph divided by the sum of attacks to all males. If there was no attack bias toward own color for the red territorial males, the proportion of attacks toward own morph should have been 1/7, 3/7, 5/7, and 6/7 in respectively the 2/8, 4/8, 6/8, and 7/8 proportion of red males treatment; the equivalent expected proportions were calculated for the blue territorial males. For each morph, separately we tested for an own-morph attack bias by testing the attack proportions (averaged at the assemblage level, meaning that response(s) of male(s) of one color were averaged in each assemblage) against the expected proportions if there were no attack bias using an HLM (three daily scores nested within each assemblage). We included proportion of red males as a covariate in the analysis.

We asked whether red and blue males differed in attack rate (per hour) given their dominance rank (see below). Note that this is not a test of relative dominance and that controlling for dominance rank enabled us to compare inherent aggression levels between color morphs while accounting for the higher aggressiveness of more socially dominant males. We calculated the dominance rank for each male and day separately based on ranking the Win Ratios within assemblages, whereby the male with dominance rank 1 had the highest Win Ratio and the male with dominance rank 8 the lowest Win Ratio. To eliminate variation in attack rates across days (Dijkstra et al. 2009), we calculated z-scores of $\ln(x + 1)$ transformed attack rates for all males in each assemblage and day of observation separately. We used an HLM, comparing daily aggression rates for each day of observation that a fish was territorial, for each individual fish that at least once attained territorial status in an assemblage (i.e., up to three daily scores were nested within individuals, which were nested within replicate assemblages). We included color morph as a factor and proportion of red males and dominance rank as covariates in the analysis.

Proportions were arcsine square-root transformed and attack rates were $\ln(x + 1)$ transformed to meet assumptions of parametric testing. Statistical analyses were carried out with SPSS 12.0.1 (SPSS Inc., Chicago, IL), except for the hierarchical linear models (HLM), which was carried out in Mlwin 2.0 (Bryk and Raudenbush 1993). All reported probabilities are for two-tailed tests of significance, unless stated otherwise. In all analyses, we also tested for possible effects of day of observation, but these are not reported here because none were significant. Although analyses accommodated possible variation in the response variable across days of observation, to simplify graphical presentation we plotted the mean (±SE) based on the pooled data across the three days of observation unless stated otherwise.

SIMULATION STUDY

In the experiment, we found that red males were socially dominant only when rare, while blue males were not socially dominant when rare. In addition, we confirmed the own-morph attack bias in both red and blue males and a higher attack rate by red than blue (see below). As these results leave scope for different interpretations as to how they can come about we decided to model the system in order to disentangle the expected effects of (1) own-morph bias in aggression and (2) morph-specific aggressiveness (which positively influences likelihood of winning a dyadic contest) on social dominance. Several parameters were set in a way such that the model closely *mimics* the study system, enabling us to vary the behavioral tendencies of interest. These model parameters concern morph differences in the distribution of aggressiveness and the dominance rank-dependent distribution in the number of fights initiated. Parameter values are based on independent datasets of agonistic behavior of *Pundamilia* and are specified below.

In the model, there are two different morphs, red and blue. For each individual male, we drew a random number from a continuous normal distribution with mean μ and standard deviation σ to represent his aggressiveness (or fighting ability), a_i. To reflect the higher aggressiveness of red relative to blue (Dijkstra et al. 2005, 2006), which determines who wins a contest dyadic contests (see below), these parameters were set to $\mu + \tau$ and σ for red males, and μ and 0.5σ for blue males (the standard deviation of aggressiveness of blue males has been found to be lower than that of the red males in a range of different experimental settings, see e.g., Dijkstra et al. 2006). To mimic the observation that a small fraction of individuals are generally more aggressive than the others, these distributions, originally symmetric around μ, were then made asymmetric by taking the absolute values of each a_i creating a skewed distribution of aggressiveness scores, with a lower bound of 0. We varied τ in the model to analyze the effect of a morph difference in the likelihood of winning dyadic contest on social dominance.

Another key parameter in the model is the probability of an individual fighting another individual belonging to the same morph, ρ. When $\rho = 0.5$, it corresponds to no bias (fighting either morph is equally likely), while values 0–0.5 or 0.5–1 correspond to avoiding or preferring an individual of the same morph to fight with. We varied ρ to analyze the influence of the own-morph aggression bias on social dominance.

To imitate the experimental setting (see above), we simulated eight individuals, out of which one, two, four, six, or seven were

red. For each round of the simulation, i.e., when each fish undergoes the pairwise agonistic interactions allocated to him, values of a_i were drawn independently as described above, and each individual initiated a number of fights against other individuals so that the most aggressive individual (i.e., with the highest a_i value) had a number of fights F drawn from a gamma distribution with the shape and scale parameters set to 5 and 20, respectively. These values were chosen such that the resulting gamma distribution matches the real distribution of the number of fights by the dominant individual in a group (Dijkstra et al. 2008a, 2009). The other individuals initiated fights according to $F^{\frac{1}{2^{x-1}}}$ (rounded to the nearest integer) where x = ranks 2 to 8 (according to a_i), resulting in a biased distribution of fights initiated, and this number increasing with increasing dominance—a pattern typically observed in haplochromine communities (Dijkstra et al. 2008a, 2009). Each fight initiated was against a less aggressive individual with probability P and against an equally or more aggressive individual with probability $1 - P$ (and, as said earlier, against own morph with probability ρ). Parameter P was set at 0.9, as we know that in social groups cichlid males preferentially attack subordinate individuals (P.D. Dijkstra, unpubl. ms.). The more aggressive individual (with higher value of a_i) had probability w (specified in results section) to win the dyadic interaction regardless of which one initiated it. After all the fights in a simulation round the Win Ratio of each morph was calculated (for details on the Win Ratio, see Data analysis), and each parameter combination was repeated 1000 times.

Results

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Own-morph attack bias and morph differences in attack rate

For each morph we plotted the proportion of attacks initiated by males toward their own morph as a function of the proportion of red males, and compared this to the no-bias line (see Fig. 1). Not surprisingly, the effect of proportion of red males was significant, because the encounter rate and thus the opportunity of attack depends on the ratio of red versus blue (HLM, proportion of red males for blue males: deviance = 44.54, df = 1, $P < 0.001$; for red males: deviance = 60.25, df = 1, $P < 0.001$). More interestingly, males significantly biased their attacks toward their own morph in both cases (HLM, observed against expected, $n = 72$ blue males, deviance 43.33, df = 1, $P < 0.001$; $n = 71$ red males, deviance = 47.71, df = 1, $P < 0.001$).

After controlling for the effect of dominance rank (HLM, deviance = 101.03, df = 1, $P < 0.001$), we found that red males were more aggressive than blue males (Fig. 2, color morph effect, deviance = 11.14, df = 1, $P < 0.001$, $n = 72$ blue; $n = 71$ red males). However, proportion of red males did not have a significant effect on attack rate (proportion of red males, deviance = 0.075, df = 1, $P = 0.78$).

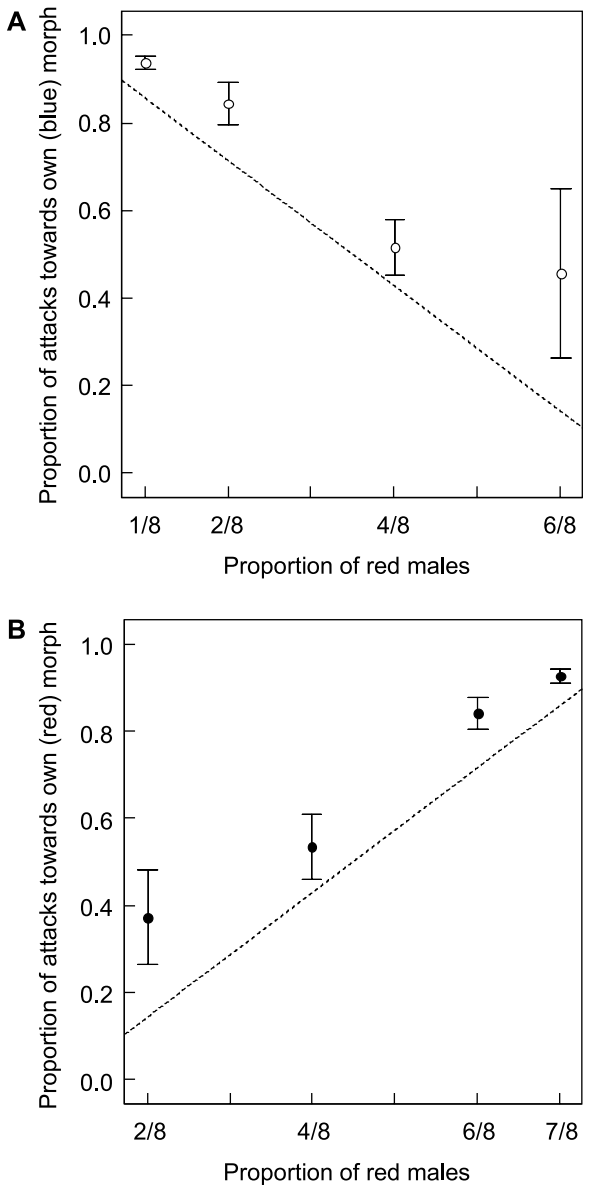

Figure 1. Results from the experimental data on cichlids showing the observed proportion of attacks by territorial males toward their own morph (mean ± SE) as a function of the proportion of red males (out of a population size of 8). Data shown separately for (A) blue and (B) red males, based on the average of the individual responses across the three days of observation. Dashed line indicates the predicted ratio if there was no bias. Males of both color morphs bias aggression toward their own color (for statistics, see text).

Frequency-dependent dominance

Symmetric negative frequency-dependent dominance would predict a negative relationship in both color morphs between their relative abundance in the population and Win Ratio. Although

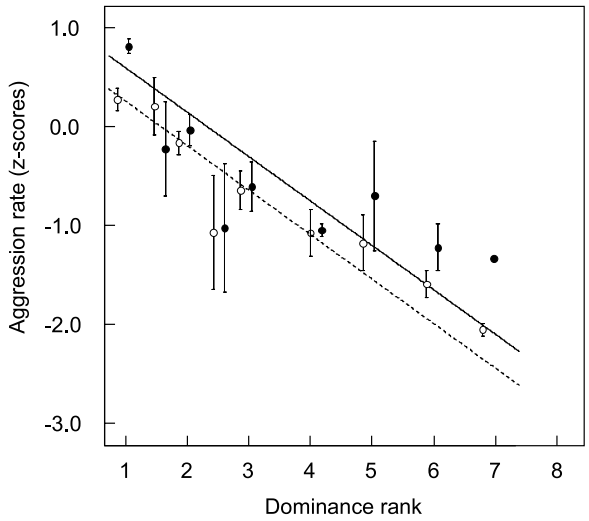

Figure 2. Results from the experimental data on cichlids showing the observed rate of attacks (z-scores) of territorial males as a function of their dominance rank (1 is most dominant); regression is fitted for blue males (empty symbols) and red males (filled symbols) separately. Red males (solid line) performed more attacks at a given dominance rank than blue males (dashed line). Shown are the mean ± SE, based on scores of individual males. Note that in contrast to other figures we could not pool the data of the three days of observation, because males could change dominance rank and sometimes even status across days of observation. Although we accounted for this in our analysis, for graphical purposes we show each daily observation individually.

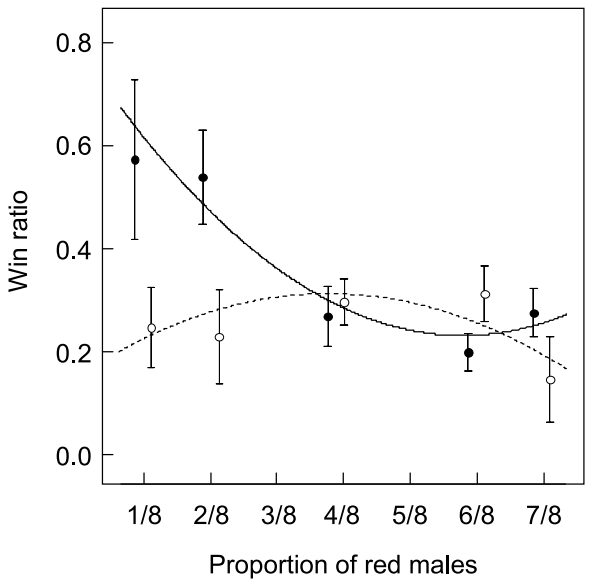

Figure 3. Results from the experimental data on cichlids showing the Win Ratio of blue (empty symbols) and red males (filled symbols) (mean ± SE) as a function of the proportion of red males (out of a population size of eight). The data are based on the median Win Ratio of blue and red males of each assemblage per day, because the Win Ratios within assemblages were skewed. The figure is based on the average of the three daily scores. Note that the mean of the Win Ratio is lower than 0.5, because the average Win Ratio for both colors is influenced by interactions with males of both own and opposite color.

there was a significant linear relationship between the Win Ratios of red males and the proportion of red males in the predicted direction (Fig. 3, HLM, proportion of red males, deviance = 32.01, df = 1, $P < 0.001$, $n = 42$ assemblages), this was not the case for blue males (proportion of red males, deviance = 0.36, df = 1, $P = 0.55$). Rather, both curves apparently took the form of a curvilinear function, which was supported by an improved fit of the model (as indicated by a reduction in the deviance) when the quadratic term of proportion of red males was added in the model for both red (HLM, quadratic term, deviance = 8.39, df = 1, $P < 0.01$) and blue males (quadratic term, deviance = 5.25, df = 1, $P = 0.02$). The curves of red and blue have opposite shapes. When examining the difference between the Win Ratio of red and blue males, it appears that red males show a tendency to be more socially dominant when rare, but otherwise the dominance of red and blue males are similar (Fig. 3). This is also supported by comparing the median Win Ratios of red and blue males; to increase power we averaged the three daily scores and combined the two extreme treatments, defining 1/8 and 2/8 as rare, 4/8 as intermediate, and 6/8 and 7/8 as abundant. The Win Ratio of red was significantly higher when rare (paired t-test, $t_{13} = 2.41$, $P = 0.03$), but not when intermediate ($t_{11} = -0.42$, $P = 0.68$) or abundant ($t_{15} = 0.65$, $P = 0.53$).

SIMULATION STUDY

The simulation study was designed to mimic the experimental situation in order to determine whether we can interpret the observed pattern in terms of an own-morph aggression bias and different likelihoods of winning dyadic contests by both morphs. The output of the models show that the expected pattern of the Win Ratios of blue and red males against the proportion of red males depends on both parameters τ (the difference in aggressiveness that determines the strength of the tendency of red males to socially dominate blue in dyadic contests) and ρ (the degree of own-morph fighting bias) (Fig. 4, see also figure caption). When red has a higher tendency to dominate blue in dyadic contests ($\tau > 0$), then red is more dominant over the entire frequency range of red in the population if there is no own-morph fighting bias (Fig. 4B). Importantly, an own-morph fighting bias substantially reduced the Win Ratio of red when they become more abundant (compare Fig. 4B, where $\rho = 0.5$, with 4d where $\rho > 0.5$). Irrespective of the strength of the tendency of red males to dominate blue in dyadic contest (τ), the Win Ratios become more strongly dependent on the proportion of red males when males of both color morphs preferentially fight their own morph, with red males being particularly socially dominant when rare (see Figs. 4C and D). The simulation suggests that when red and blue have equal

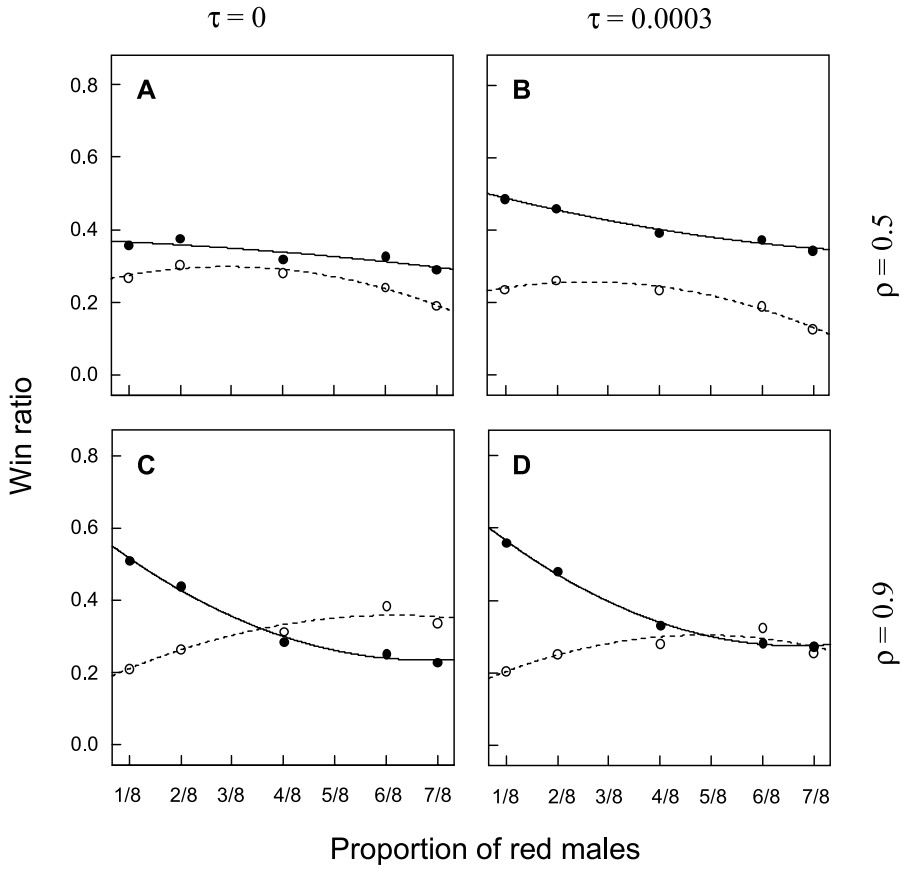

Figure 4. **Results from the simulation study showing variation in the Win Ratios of blue (empty symbols) and red males (filled symbols) in relation to the proportion of red males in the population (out of a population size of eight). The four different panels show the simulation results for differing parameters values of τ (difference in aggressiveness which determines the extent to which red males are socially dominant over blue in dyadic contests) and ρ (the degree of own-morph attack bias). Dots show the means of 1000 simulation rounds for the red and blue males. The other parameter values used here were: μ = 0.0001 (mean aggressiveness), *P* = 0.9 (probability that the fight was initiated against a less aggressive individual), and *w* = 0.9 (probability that the more aggressive individual wins the fight). Curvilinear regression fits for red (solid line) and blue males (dashed line) are also shown in each panel. It should be noted that the small difference in Win Ratios between red and blue in panel 4A disappears when the standard deviation in aggressiveness is set equal for the two color morphs. See text for further explanation.**

tendencies to win dyadic contests, an own-morph fighting bias can actually result in rare-morph social dominance advantages to both color morphs (Fig. 4C). However, curvilinear regression fits of the relationships between Win Ratios and proportion of red males suggest that expected patterns are not simply linear. In conclusion, it appears that a combination of the tendency of red males to socially dominate blue males in dyadic contest and own-morph fighting bias results in social dominance of red when they are rare, but not for blue when they are rare (see Fig. 4D). An interesting finding is that the model output in Figure 4D resembles the pattern in Win Ratio observed in our experiment (Fig. 3), giving support to the idea that the interaction between the difference in aggressiveness and own-morph fighting bias is the key in understanding the experimental results.

Finally, it should be noted that the frequency-dependent pattern observed in panel 4A disappears when the standard deviation in aggressiveness is set equal for the two color morphs.

Discussion

In order to explain the coexistence of different color morphs we set out to test whether symmetric negative frequency-dependent selection, i.e., rare advantages to both male types, can arise from social dominance competition in two cichlid color morphs. As expected, we found that red males were socially dominant over blue when rare, and less so when more abundant. However, in contrast to expectation, blue males were not socially dominant over red when rare. We then confirmed two important behavioral properties of our study species that could help us understand the observed pattern in frequency-dependent social dominance. First, red and blue males biased aggression toward opponents of their

own color morph, confirming previous findings (Dijkstra et al. 2006, 2008b, 2009; Verzijden et al. 2009). Secondly, we found that for the same dominance rank, red males had still a higher rate of attack than blue males, suggesting that red males are inherently more aggressive than blue males, consistent with previous studies in which red males were more aggressive and more likely to defeat blue males in dyadic contests (Dijkstra et al. 2005, 2006, 2009).

The simulation study mimicked the experimental setting and explored how two important behavioral properties or rules with regard to choice of opponent and different likelihoods of winning dyadic contests could influence the dynamics of frequency-dependent social dominance between two color morphs. When the red morph has a higher tendency to dominate blue in dyadic contests then red is predicted to dominate blue over the entire frequency range in the population. Notably, in the simulation we found that when males show an own-morph attack bias, red males are socially dominant over blue when they are rare, but considerably less so when red increases in frequency. Additionally, the simulation shows that the social dominance of red males in dyads prevents blue males from attaining a social dominance advantage when rare, despite an own-morph attack bias. It appears that two simple aspects of agonistic behavior (own-morph attack bias and different likelihoods of winning dyadic contests) can help explain our experimental findings.

Male contest competition has been hypothesized to generate negative frequency-dependent selection, explaining why differently colored congeners can coexist (Seehausen and Schluter 2004; see also Partridge and Hill 1984; Grether et al. 2009). Previous studies proposed the possibility of negative frequency-dependent social dominance between competing color morphs, whereby *both* color morphs should enjoy higher dominance when rare (Dijkstra et al. 2006). Our experimental test is inconsistent with such a symmetric rare-morph dominance advantage and rather indicates that the rare-morph dominance advantage is one-sided and restricted to the red, socially dominant morph in the species that we studied. Keeping the simulation results in mind, we hypothesize that the higher aggressiveness of red males (which determines the extent to which red males are socially dominant over blue in dyadic contests) helped red males in our experiments to attain higher dominance status than blue males when the red morph was rare. The reduced social dominance of red males when occurring at higher proportions (4/8, 6/8, 7/8) is likely due to the own-morph attack bias leading to more competition among red males in which they obviously lack the advantage of red-blue fights. We did not include self-reinforcing effects, such as winner-loser effects in the interpretation of our findings (see e.g., Hemelrijk and Wantia 2005; Hsu et al. 2006), although it is likely these effects are relevant too. For example, in a study on intersexual dominance in groups of primates, it was found that in groups with a higher percentage of males, females become socially dominant over males than in groups with fewer males (Hemelrijk et al. 2008). These findings could be explained by self-reinforcing winner-loser effects, in particular the heavy losses males suffered in groups with plenty of males. Studying how winner-loser effects affect the social dominance dynamics in our cichlid study system would be an interesting avenue for future research (e.g., Oliveira et al. 2009).

An important conclusion from our study is that despite a lack of evidence for symmetric negative frequency-dependent social dominance, aggressive competition can result in frequency-dependence in social dominance between color morphs and as such it may *contribute* to coexistence of different morphs (Seehausen and Schluter 2004). Selection arising from male contest competition can be strong in haplochromines since only territorial males have access to ripe females and territory quality influences mate choice (Maan et al. 2004; Dijkstra et al. 2008a). The restriction of the rare-male dominance advantage to red may indeed help explain field data. Whereas *Pundamilia* populations are often entirely composed of blue males, red *Pundamilia* males without exception occur sympatrically with blue ones (Seehausen and Van Alphen 1999). We hypothesized earlier that a social dominance advantage of red may help them to invade blue populations (Dijkstra et al. 2005). However, other factors are likely necessary to keep red males at bay. In the Gouldian finch, Pryke et al. (2007) found that highly aggressive red-headed males were more dominant socially, but had reduced immunocompetence compared with the less aggressive black-headed males when red-headed males were frequent in the population. It is possible that there is a physiological cost to the red *Pundamilia* morph too (see also Clotfelter et al. 2007). In addition, in *Pundamilia*, red males might be more easily detected by predators, although this remains untested (Maan et al. 2008).

It is important to note that rare-male advantages arising from male contest competition may also emerge in other ways (Seehausen and Schluter 2004; Hemelrijk et al. 2008). For example, rare males may benefit from less costly competition by being able to maintain above-average physical condition or to allocate more time and energy to courtship displays (Seehausen and Schluter 2004). In one of our previous studies, we also hypothesized that rare males are more likely to obtain high-quality territories, which play a key role in mate-choice decisions (Dijkstra et al. 2008a).

Apart from the study on primates (Hemelrijk et al. 2008), frequency-dependent social dominance has not been directly addressed before, although it could be implicated in studies looking at frequency-dependent effects on fitness (Horth 2003; Olendorf et al. 2006; Bleay et al. 2007; Fuller and Johnson 2009). Olendorf and co-workers (2006) found frequency-dependent survival within highly variable guppy populations. Although the authors mainly attribute this to a decreased probability of predators

detecting rare prey types, an alternative mechanism is that male guppies with rare colors experience reduced intraspecific competition; more studies are needed to elucidate the different factors that generate the frequency-dependent selection within these guppy populations (Nosil 2006).

In this study, we explored frequency-dependent effects of social interactions emerging from own-morph attack biases and different likelihoods of winning dyadic contests between two color morphs. Although our experiment was done with cichlids, and is relevant to our understanding of the spectacular radiation of haplochromine cichlid fish in the Great African Lakes, we believe that our findings have wider implications. Many animal species preferentially direct agonistic behaviors toward similarly colored rivals (fish: Losey 1982; Pauers et al. 2008; birds: Alatalo et al. 1994; insects: Tynkkynen et al. 2004; Anderson and Grether 2009). Asymmetric dyadic dominance relationships are also widespread (fish: Barlow 1983; Horth 2003; Kingston et al. 2003; Korzan and Fernald 2007; birds: Owen-Ashley and Butler 2004; Pryke and Griffith 2006; lizards: Calsbeek and Sinervo 2002b; Healey et al. 2007). We therefore believe that our findings have general bearing on understanding the selective forces that maintain phenotypic and genetic variation.

ACKNOWLEDGMENTS

We thank Dagmar Heidinga and Ruthy Fraterman for help with the experiment. Mhoja Kayeba, Mohamed Haluna, John Mrosso, and Martine Maan are acknowledged for fish collection. The research was financed by the Netherlands Organisation for Scientific Research, NWO (SLW) grant 810.64.013 to TGGG, a Rubicon grant 825.07.00, and a European Commission Marie Curie Outgoing International Fellowship grant to PDD, and a grant from the Swiss Science Foundation to OS. The research was carried out with an animal experiment license (DEC 2812) from Groningen University and complied with current laws in The Netherlands.

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Associate Editor: S. West

Supporting Information

The following supporting information is available for this article:

Figure S1. Empirical results showing the Average Dominance Index of blue (empty symbols) and red males (filled symbols) (mean ± SE) as a function of the proportion of red males (out of a population size of eight).

Supporting Information may be found in the online version of this article.

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